Revision of the Enigmatic Genus Marshiella Shaw in the New World with the Description of Three New Species (Hymenoptera: Braconidae: Euphorinae)

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Abstract.—The genus Marshiella Shaw is revised for the New World region. Included are two previously described species, Marshiella plumicornis (Ruthe) and M. pulvillicornis (Walley and MacKay), and three newly described species, M. bobella Shaw, M. lettermani Shaw, and M. marshi Marsh. A key to New World species is provided, along with species descriptions, diagnostic characters, distribution, antennal micromorphology, and phylogenetic patterns.

The euphorine braconid genus Marshiella was erected by Shaw (1985) to include two enigmatic species with unusually modified antennae that had previously been placed in other genera. Marshiella plumicornis (Ruthe) was formerly placed in Microctonus Wesmael (Shenefelt 1969), while M. pulvillicornis (Walley and MacKay) was previously placed in Streblocera Westwood (Walley and MacKay 1963), but Shaw (1985) demonstrated that these species were closely related based on the uniquely modified, densely setose basal flagellomeres (Figs. 1-2) and must be assigned to a new genus. Previously the genus was known only from the Holarctic region, extending as far south as Mexico in the New World (Shaw 1985). More recently the genus has been recorded as far south as Costa Rica (Shaw 1997) and two new species have been recently described from China (Chen and van Achterberg 1997) extending the known distribution to the Oriental region. In this paper the New World species are reviewed and three new species are described including material from Arizona, Texas, Mexico, Costa Rica, and Brazil.

A full generic diagnosis for the genus *Marshiella* has been published by Shaw (1985) and more recently by Chen and van Achterberg (1997), so it is not necessary to repeat that information here. Recognition of the genus is quite easy as it is the only braconid with flagellomeres 1–4 or 1–5 flattened and densely setose ventrally (as in Figs. 1–2, 5–6, 10–16, 18–19). Specimens can be keyed to genus using the keys provided by Shaw (1985), Chen and van Achterberg (1997), or Shaw (1997).

Very little is known about the biology of *Marshiella* species, but they are presumed to be koniobiont endoparasitoids of adult Coleoptera as are most other basal clades of the Euphorinae (Shaw 1985, 1988; Shaw and Huddleston 1991). Only one species, *M. plumicornis* (Ruthe) has been reared from a host, an anthicid beetle, *Notoxus monoceros* L. (Smith 1953; Gornitz 1937). The same species has been collected at cantharadin-baited traps in Michigan, indicating that *Marshiella* species probably orient to their hosts using chemical cues (Shaw 1985; Dettner 1997). Mostly *Marshiella* species are quite rare, with

the Canadian species *M. pulvillicornis* (Walley and MacKay) and the two Chinese species, *M. binarius* Chen and van Achterberg and *M. sinensis* Chen and van Achterberg, being known only from the holotypes. However, two of the new species treated in this paper have been collected in series from Malaise traps in Costa Rica, and occasionally are attracted to lights. Males are totally unknown. The function of the modified flagellum in *Mar*-

shiella females has not been observed, but its form suggests the possibility that it is an adaptation for grasping the host beetle during oviposition since female euphorines oviposit by swinging the metasoma ventrally and anteriorly and exserting the ovipositor forward between the legs and in front of the face of the advancing wasp.

Authorship for new species is by either Shaw or Marsh, as indicated for each species.

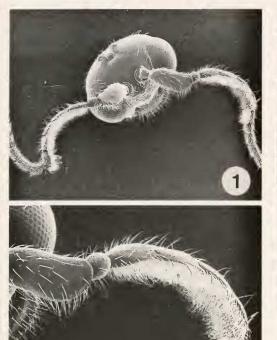
KEY TO THE FEMALES OF NEW WORLD SPECIES OF MARSHIELLA SHAW

| | Dorso-lateral areas of propodeum entirely rugulose (Fig. 3); flagellomeres 2–4 in dorsal view only slightly broader than flagellomeres 8–10 |
|----|---|
| - | Dorso-lateral areas of propodeum entirely smooth and highly polished (Fig. 4); flagellom- |
| | eres 2–4 in dorsal view strongly widened and heart-shaped (Figs. 5–6), about 2× broader than flagellomeres 8–10 |
| 2. | Flagellomere 5 in dorsal view nearly cylindrical, and only slighter wider than flagellomere |
| | 6, not strongly flattened |
| _ | Flagellomere 5 in dorsal view strongly flattened, distinctly heart-shaped and nearly 2× |
| | broader than flagellomere 6 |
| 3. | Body size very small, less than 2 mm long; antenna short, with only 17 flagellomeres; |
| | mesosoma reddish brown; known only from Canada |
| | Marshiella pulvillicornis (Walley and MacKay) |
| - | Body size larger, more than 2 mm long; antenna longer, with 19–21 flagellomeres; meso- |
| | soma jet black; known only from Costa Rica Marshiella lettermani Shaw, new species |
| 4. | Metasomal tergum 1 entirely smooth on posterior half, beyond spiracles; ocellar-ocular |
| | space pale yellowish white; known only from Brazil |
| | Marshiella marshi Marsh, new species |
| _ | Metasomal tergum 1 finely rugulose on posterior half, beyond spiracles; ocellar-ocular |
| | space entirely or partly dark chocolate brown to black; know from Arizona, Texas, Mexico, |
| | and Costa Rica Marshiella bobella Shaw, new species |

Marshiella bobella Shaw, new species (Figs. 1–2, 4, 6, 8, 12–13)

Description of holotype female.—Body length 2.3 mm; forewing length 2.3 mm; ovipositor length 1.1 mm. Color: frons, vertex, temple, and entire mesosoma black; flagellomeres 1–5 dorsally, remainder of flagellum, wing venation, entire metasoma and ovipositor sheath dark chocolate brown; scape, pedicel, flagellomeres 1–5 ventrally, remainder of head, legs entirely, and ovipositor light yellowish brown; eye silvery gray; wing mem-

brane hyaline; setae, especially on flagellomeres 1–5 ventrally, pale silvery white. Head: scape 2.3× longer than wide, apical ventral margin protruding and carinate longitudinally; flagellomeres 1–5 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae (Figs. 12–13); flagellomere 1 2× longer than wide; flagellomere 2 about as long as wide; flagellomeres 3–4 slightly wider than long; flagellomere 5 smaller, about as long as wide; remainder of flagellum comprising 15 flagellomeres of



Figs. 1–2. *Marshiella bobella* Shaw, anterior view. 1, head and antennae. 2, basal section of antenna showing modified flagellomeres 1–5.

normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 5× width of lateral ocellus. Mesosoma: mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae; scutellar furrow 2foveate; scutellar disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and finely-foveate sternaulus; length of marginal cell 0.6× length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by V-shaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and





Figs. 3–4. Propodeum, dorso-lateral view, $220 \times .3$, Marshiella plumicornis (Ruthe). 4, Marshiella bobella Shaw.

shining. **Metasoma:** petiolate tergum 1 narrow basally, then gradually wider, posterior width 3× wider than extreme basal width; petiole 7× longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose; remainder of metasoma smooth and highly polished; ovipositor length 2× length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Variation.—paratype females appearing similar to holotype except apical 'normal' section of flagellum with 14 or 15 flagellomeres. The ovipositor is extremely flexible and varies in appearance depending on its position at death. Ovipositor shape varies from curved along basal ½ to nearly straight. Depending on the degree to which the tip of the metasoma is flexed ventrally and anteriorly the ovipositor base may appear to emerge apically or

ventrally near the mid-point of the metasoma. The specimens from Texas have less dark brown color on the top of the head, but otherwise agree with the diagnosis of this species.

Material examined.—Holotype female: Costa Rica, San Jose Province: Zurqui de Moravia, 1600 m, April 1992, P. Hanson, Malaise trap, deposited at University of Wyoming. Paratype females: 1 same data as holotype; 1 same data except July 1990; 6 same data except November-December 1990; 1 same data except May 1992; 3 same data except June 1992; 1 same data except July 1992; 1 same data except February 1996. Cartago Province: 1, La Cangreja, 1950m, July 1991, P. Hanson, Malaise trap; 1 same data except June-July 1992. Guanacaste Province: 1, P. N. Guanacaste, 9 km S Santa Cecilia, Estacion Pitilla, 700 m, 2-19 March 1992, P. Rios, INBio barcode CR1000-420531; 1 same data except 31 March-15 April 1992, INBio barcode CR1000-771575; 1, Tierras Morenas, 700m, December 1992, G. Rodriguez, INBio barcode CR1001-288145; 1, Santa Rosa National Park, 300 m, 14 August-6 September 1986, I. D. Gauld and D. Janzen, Malaise trap, Bosque Humedo, mature evergreen dry forest, fully shaded. Mexico: 1, Chis., L. Montebello National Park, 5000 ft., 30 May 1969, Malaise trap. U.S.A.: 1, Arizona, 5 mi. W Portal, 7 July 1956, O. L. Cartwright, light trap; 2, Texas, Sabine Co., 9 mi. E. Hemphill, 23 June to 2 July 1989, Anderson and Morris, flight intercept trap in beech/magnolia forest. Paratypes deposited at University of Wyoming, Universidad de Costa Rica, Instituto Nacional de Biodiversidad, Texas A&M University, and U.S. National Museum of Natural History.

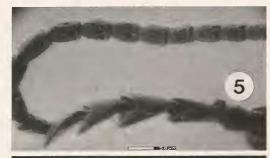
Comments.—Specimens of this species from Arizona and Mexico had been previously treated as variations of *M. pulvillicornis* by Shaw (1985), but the substantial series of specimens now available from Costa Rica show this to be a distinct species most easily separated by its having

flagellomere 5 modified along with flagellomeres 1–4, larger body size, and longer flagellum. The only other *Marshiella* species with flagellomere 5 modified is *Marshiella marshi* from Brazil, which can be distinguished by its smooth metasomal tergum 1 and lighter head color.

Etymology.—The species name is an arbitrary combination of letters to form a euphonious combination.

Marshiella lettermani Shaw, new species (Figs. 14–16)

Description of holotype female.—Body length 2.9 mm; forewing length 2.8 mm; ovipositor length 1.3 mm. Color: frons medially, ocellar triangle, and entire mesosoma except prosternum black; flagellomeres 1-4 dorsally, remainder of flagellum, prosternum, wing venation, entire metasoma and ovipositor sheath dark chocolate brown; scape, pedicel, flagellomeres 1-4 ventrally, remainder of head, legs entirely, and ovipositor very pale yellowish brown; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1-5 ventrally, pale silvery white. Head: scape 2.3× longer than wide, apical ventral margin protruding and carinate longitudinally; flagellomeres 1-4 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae on flagellomeres 1 and 4, shorter bent Velcro-like setae on flagellomeres 2-3 (Figs. 14–16); flagellomere 1 2× longer than wide; flagellomere 2 about as long as wide; flagellomere 3 slightly wider than long; flagellomere 4 smaller, about as long as wide; remainder of flagellum comprising 17 flagellomeres of normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 3.5× width of lateral ocellus. Mesosoma: mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae; scutellar furrow 2-foveate; scutellar



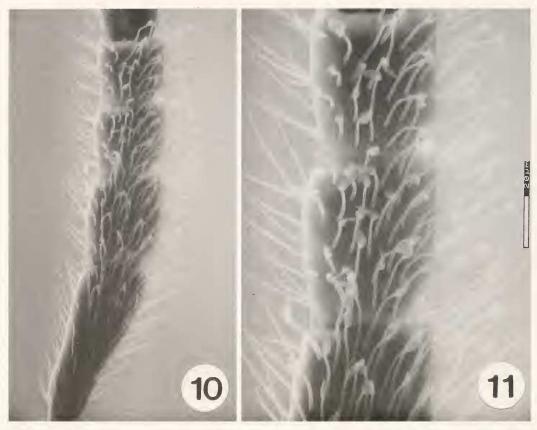


Figs. 5–6. Basal section of antennal flagellum, dorsolateral view. 5, Marshiella pulvillicornis (Walley and MacKay), $230\times$. 6, Marshiella bobella Shaw, $235\times$.

disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and coarsely-foveate sternaulus: length of marginal cell 0.9× length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by Vshaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and shining. Metasoma: petiolate tergum 1 narrow basally, then gradually wider, posterior width 2.8× wider than extreme basal width; petiole $6 \times$ longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose on basal 3/4; posterior 1/4 of petiole and remainder of metasoma smooth and highly polished; ovipositor length 1.9× length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.



Figs. 7–9. Metasomal tergum 1, dorso-lateral view. 7, Marshiella plunicornis (Ruthe), 220×. 8, Marshiella bobella Shaw, 195×; 9, Marshiella marshi Marsh, 220×.



Figs. 10–11. *Marshiella plumicornis* (Ruthe), basal section of antennal flagellum, ventral view. 10, flagellomeres 1-5, 295×11 , detail of flagellomeres 1-3 showing spatulate setae, 700×10^{-5} .

Variation.—paratype females appearing similar to holotype except apical 'normal' section of flagellum with 15 to 17 flagellomeres, body size 2.2 to 2.9 mm, and dark brown covering most of frons and vertex.

Material examined.—Holotype female: Costa Rica, Puntarenas Province: San Vito, Estacion Biological Las Alturas, 1500 m, December 1991, P. Hanson, Malaise trap, deposited at University of Wyoming, Laramie. Paratype females: 1 same data as holotype; 1 same data except November 1991; 2 same data except June 1992. Paratypes deposited at University of Wyoming and Universidad de Costa Rica.

Comments.—Marshiella lettermani is most similar to M. pulvillicornis (Walley and MacKay) in that both of these species have

flagellomeres 1–4 greatly widended and densely setose, but flagellomere 5 is not so modified. The Costa Rican species *M. lettermani* can be distinguished from *M. pulvillicornis* by its larger body size (nearly 3 mm), black mesosoma, short bent Velcrolike setae on flagellomeres 2–3 (Fig. 16), and longer flagellum with 19–21 flagellomeres. *M. pulvillicornis* is much smaller (less than 2 mm), has a reddish brown mesosoma, shorter flagellum with only 17 flagellomeres, entirely long wispy flagellar setae, and is known only from Canada.

Etymology.—The species name is a patronym for David Letterman, host of the Late Show, in appreciation for his outstanding contributions to late night entertainment. Many a dull day has been im-





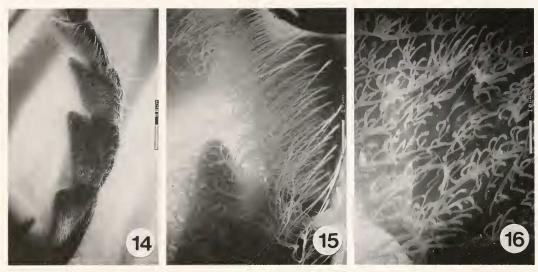
Figs. 12–13. *Marshiella bobella* Shaw, basal section of antennal flagellum, ventral view. 12, flagellomeres 1–5, 215×. 13, detail of flagellomere 5 showing long wispy setae, 905×.

proved by his humor. It somehow seems appropriate that a really weird insect should be named in his honor.

Marshiella marshi Marsh, new species (Figs. 9, 17–19)

Description of holotype female.—Body length 2.9 mm; forewing length 2.8 mm; ovipositor length 1.2 mm. Color: frons, vertex, and temple medially light brown; margins of ocelli and notauli black; flagellomeres 1-5 dorsally, remainder of flagellum, wing venation, mesosoma except prosternum, metasoma except petiole basally, and ovipositor sheath dark reddish brown; scape, pedicel, flagellomeres 1-5 ventrally, remainder of head, legs entirely, and ovipositor very pale yellowish brown to yellowish white; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1–5 ventrally, pale silvery white. Head: scape 3.0× longer than wide, apical ventral margin protruding (Fig. 17) and carinate longitudinally; flagellomeres 1-5 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae, some of which are intertwined or braided (Figs. 18-19); flagellomere 1 1.5× longer than wide; flagellomere 2 about as long as wide; flagellomeres 3-4 slightly wider than long; flagellomere 5 smaller, about as long as wide; remainder of flagellum comprising 15 flagellomeres of normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 4× width of lateral ocellus. Mesosoma: mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae medially; scutellar furrow 2-foveate; scutellar disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and finely-foveate sternaulus; length of marginal cell 0.7× length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by Vshaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and shining. Metasoma: petiolate tergum 1 narrow basally, then gradually wider, posterior width 3× wider than extreme basal width; petiole 7× longer than wide at extreme base; dorsal surface of basal 1/2 of petiole finely longitudinally rugose; posterior 1/2 of petiole and remainder of metasoma smooth and highly polished; ovipositor length 2× length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Material examined.—Holotype female: Brazil, Rondonia, Vilhena, 21 degrees 40 minutes S, 60 degrees 08 minutes W, October 1973, M. Alvarenga, deposited at Canadian National Collection, Ottawa.



Figs. 14–16. *Marshiella lettermani* Shaw, basal section of antennal flagellum, ventral view. 14, flagellomeres 1–5, 215×. 15, flagellomeres 3–4, 745×, showing variation of seta form and density. 16, flagellomere 3, 1450×, showing detail of short, bent, Velcro-like setae.

Comments.—Marshiella marshi can be separated from most other species by its having flagellomere 5 modified along with flagellomeres 1-4, larger body size, and longer flagellum. The antennal scape is slighly more protruberant and setose (Fig. 17) than other species. Some of the long wispy setae on flagellomeres 2-3 are intertwined or braided (Fig. 18-19), but the sample size is too limited to determine if this is natural or a post-mortem effect of preservation methods. The only other Marshiella species with flagellomere 5 modified is M. bobella from Arizona, Costa Rica, and Mexico, which can be distinguished from M. marshi by its rugulose metasomal tergum 1 and darker head color.

Etymology.—The species is named in honor of Jon Marsh, son of the junior author.

Marshiella plumicornis (Ruthe) (Figs. 3, 7, 10–11)

Microctonus plumicornis Ruthe, 1856. Reclassified by Shaw, 1985.

Description of female based on North American material.—Body length 1.8–1.9 mm;

forewing length 1.7–1.8 mm; ovipositor length 0.6–0.7 mm. Color: frons, vertex, temple, gena, mesosoma except pronotum and prosternum, flagellomeres 4-16, wing venation, entire metasoma and ovipositor sheath dark chocolate brown to black (fading to yellowish brown in old specimens); scape, pedicel, flagellomeres 1-3, remainder of head, legs entirely, and ovipositor light yellowish brown; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1-4 ventrally, pale silvery white. Head: scape 2.2× longer than wide, apical ventral margin not protruding or carinate longitudinally; flagellomeres 1–4 modified, pulvilliform, narrowly heart-shaped in dorsal view, ventrally densely setose with setae expanded and flattened apically into spatulate tips (Figs. 10–11); flagellomere 1 3× longer than wide; flagellomeres 2-3 about 2× as long as wide; flagellomere 4 1.5× wider than long; remainder of flagellum comprising 12 flagellomeres of normal form; face not protruding below antennal insertions; eyes convergent ventrally, closest near ventral margin of face; ocelli small, ocellar-ocular distance 5× width of lateral



Figs. 17–19. *Marshiella marshi* Marsh, basal section of antenna. 17, scape and pedicel, lateral view, $380 \times$. 18, flagellomeres 1–5, ventral view showing long wispy setae, $250 \times$. 19, flagellomere 2, ventral view showing detail of intertwined, braided setae, $885 \times$.

ocellus. Mesosoma: mesoscutum smooth and highly polished except notauli foveate, median and lateral lobes mostly devoid of setae: scutellar furrow 2-foveate: scutellar disc smooth and highly polished; mesopleuron smooth and highly polished except coarsely-foveate sternaulus; length of marginal cell 0.4× length of pterostigma; rugulose dorso-lateral surfaces of propodeum margined posteriorly by Vshaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, dorso-lateral, posterior, and lateral surfaces rugulose, but somewhat polished and shining. Metasoma: petiolate tergum 1 narrow basally, then gradually wider, posterior width 3× wider than extreme basal width; petiole 5× longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose; remainder of metasoma smooth and highly polished; ovipositor length 1.6× length of tergum 1, basally emerging from longitudinal ventral slit apically to near midpoint of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Material examined.—U.S.A., Arizona: 1

female, Safford, 4 November 1955, G. D. Butler, swept from alfalfa. California: 1 female with cocoon, Chino, July 1932, A. J. Basinger, ex. peaches infested by A. lineatella. Florida: 1 female, St. Lucie Co., 31 March-5 April 1930, J. R. Barass, Florida fruit fly trap survey; 1 female, Indian River, 10 March 1930, J. R. Barass, Florida fruit fly trap survey. Michigan: 2 females, Ingham Co., Dewitt Township, 10-17 June 1982, D. K. Young, taken at cantharadin bait. 1 female, Kalamazoo Co., Harrison Lake, T3S, R12W, sec. 34, 16-26 June 1982, J. K. Young, taken at cantharadin bait. South Carolina: 1 female, Clemson, no date, G. G. Ainslie; 1 female, Clio, 22 July 1936, on cotton, lot 36-30265. Deposited at U.S. National Museum of Natural History, Washington, D.C. Holotype female from Germany examined by Shaw (1985), deposited at the Natural History Museum, London.

Comments.—This species has the widest distribution of any Marshiella species, being recorded from both Europe (Chen and van Achterberg 1997) and the United States (Shaw 1985). M. plumicornis can be easily distinguished from all other New World species of Marshiella by the dorso-

lateral areas of the propodeum being entirely rugulose and flagellomeres 2-4, in dorsal view, being only slightly wider than flagellomeres 8-10.

The distinctive flagellar setae micromorphology (Figs. 10–11), with the ventral setae of flagellomeres 1-4 having flattened, spatulate tips, was previously documented by Shaw (1985). It was previously presumed that this setal micromorphology was a characteristic of the genus Marshiella (Shaw 1985; Chen and van Achterberg 1997), however, the more complete survey presented here indicates that setal micromorphology varies among Marshiella species, and the spatulate form has so far only been documented in M. plumicornis.

Biology.—M. plumicornis has been reared from the anthicid Notoxus monoceros L. in Europe (Gornitz 1937; Smith 1953), but it has not yet been reared in North America. It has been attracted to cantharadin bait (Shaw 1985), suggesting possible chemosensory location of coleopteran hosts (Dettner 1997). Dan Young (pers. comm.) reports having seen braconids attracted to cantharadin in Michigan (presumably this species) attacking anthicids near the trap. One specimen was reared from peaches infested with the gelechiid Anarsia lineatella Zeller (the peach twig borer), but it seems unlikely that this was the actual host (more likely it was a beetle in the same substrate).

Marshiella pulvillicornis (Walley and MacKay) (Fig. 6)

Streblocera pulvillicornis Walley and MacKay, 1963. Reclassified by Shaw, 1985.

Material examined.—Holotype female, Canada, Quebec, Gatineau Park, Meach Lake, 9 June 1961, G.S. Walley, sweeping, No. 8223, deposited in Canadian National Collection, Ottawa.

Comments.—This species was described by Walley and MacKay (1963) based on a single female specimen from Quebec. No new material of the species has since been discovered, therefore there is no need to redescribe the species here. In addition to other characters mentioned in the key, this species can be distinguished from other Marshiella by its small body size (less than 2mm), short flagellum with 17 flagellomeres, and reddish brown mesosoma.

Discussion of Phylogenetic Considerations.—Our understanding of variation for characters of possible phylogenetic significance in Marshiella species is no doubt limited by the scarcity of material for several species, and also the lack of biological data for all but one species. Nevertheless, it is tempting to speculate on the possible phylogenetic interpretation of several characters, especially the unique antennal modifications which are presumptive synapomorphies by out-group comparison with the presumed sister-group, Townesilitus (Shaw 1985).

Four of the New World species appear to form a distinctive monophyletic cluster including M. bobella, M. lettermani, M. marshi, and M. pulvillicornis. Synapomorphies supporting this lineage include greatly widened and strongly flattened basal flagellomeres (Fig. 18), modified scape with the apical ventral margin protruding (Fig. 17), dorsum of propodeum with large smooth areas devoid of sculpture (Fig. 4), and face with pale coloration. Although the two Chinese species were not available for examination, the published descriptions agree more closely with the conditions seen in the more basal M. plumicornis which has more cylindrical and less flattened flagellomeres, shorter and less protruding scape, rugose propodeum, and brown face. The significance of a derived cluster including M. bobella, M. lettermani, M. marshi, and M. pulvillicornis is two-fold. First, this indicates that all the more basal species of Marshiella have holarctic or palearctic distributions, while all the species with Neotropical distributions belong to a derived strictly New World cluster. This is consistent with an hypothesis of one invasion of South America, from the north temperate zone. Second, it shows that the one species with known biology is basal, suggesting the possibility that the highly modified antennae of the more southern New World species may also be modifications for locating hosts via cantharadin or other semiochemicals.

ACKNOWLEDGMENTS

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